



A remarkable new family of stinging wasps from the Cretaceous of Myanmar and China (Hymenoptera, Aculeata)

Anderson Lepeco^{1,2}, Diego N. Barbosa¹, Gabriel A. R. Melo¹

1 *Laboratório de Biologia Comparada de Hymenoptera, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil* **2** *Laboratório de Biologia Comparada e Abelhas, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil*

Corresponding author: Anderson Lepeco (al.lepeco@gmail.com)

Academic editor: Michael Ohl | Received 20 April 2022 | Accepted 23 November 2022 | Published 20 December 2022

<https://zoobank.org/0EA310AF-8084-4448-AEDA-4CD39772A98B>

Citation: Lepeco A, Barbosa DN, Melo GAR (2022) A remarkable new family of stinging wasps from the Cretaceous of Myanmar and China (Hymenoptera, Aculeata). *Journal of Hymenoptera Research* 94: 163–190. <https://doi.org/10.3897/jhr.94.85613>

Abstract

Burmese amber provides a unique window to the Cretaceous entomofauna, being the most prolific source of fossil insects for the period. Presently, about 61% of the Hymenoptera described from amber deposits in Myanmar are stinging wasps (Aculeata), including eight families known solely from Burmese amber. In the present work we describe the aculeate family †Trifionychidae **fam. nov.**, as well as three new genera: †*Prionaspidion* **gen. nov.**, including †*Prionaspidion brevidens* **sp. nov.** and †*P. nanus* **sp. nov.**; †*Trifionyx* **gen. nov.**, including †*Trifionyx pilosus* **sp. nov.**; and †*Trifionyximus* **gen. nov.**, including †*Trifionyximus cracens* **sp. nov.** We also reinterpret the fossil genus †*Mirabythus*, described based on rock impressions from the Yixian formation in China and originally attributed to Scolebythidae. †*Mirabythus* is moved to the new family, based mainly on the characteristic mandible; the large clypeus with a series of small denticles on the apical margin; the frons protruding over lateral portions of clypeus, directing the antennal sockets downwards below ocular level; and the presence of nine flagellomeres. Based on resemblances with fossil impressions attributed to †Bethylonymidae, we tentatively include the new family within the superfamily †Bethylonymoidea. Discovery of †Trifionychidae **fam. nov.** adds a novel lineage to the pool of aculeate families from the Cretaceous which did not survive to the present day.

Keywords

Burmese amber, fossil, morphology, paleoentomology, sting, Yixian formation

Introduction

Stinging wasps (Aculeata) represent over 60,000 species, corresponding to ~43% of the total diversity of Hymenoptera (Aguilar et al. 2013). They are characterized by the possession of a sting, a unique evolutionary novelty among insects used for defense and preying, being a modification of the ovipositor to deliver venom instead of laying eggs (Snodgrass 1935). Aculeata have long been recognized as a monophyletic group supported by both morphological and molecular data (Oeser 1961; Rasnitsyn 1988; Vilhelmsen et al. 2010; Johnson et al. 2013; Peters et al. 2017).

Traditionally, these wasps are divided into three superfamilies: Chrysidoidea, Vespoidea and Apoidea, based on the phylogenetic analysis of Brothers (1975), Brothers and Carpenter (1993), and Brothers (1999). The Chrysidoidea include mostly small parasitoid wasps with reduced wing venation, with the extant diversity composed of three larger families: Bethyridae, Chrysididae and Dryinidae, as well as four rarely collected families with mostly tropical distributions (i.e., Embolemidae, Plumariidae, Sclerogibbidae, and Scolobythidae). Vespoidea is composed by a diverse assemblage of parasitoid and predatory wasps, including the highly eusocial vespids and ants, as well as the spider wasps and velvet ants. Finally, the Apoidea comprise the bees and a large array of predatory wasp lineages, and, together with the Vespoidea, are referred to as the Aculeata *sensu stricto*.

Although Brothers' (1975) classification still is in use today, recent phylogenetic analyses based on molecular data have put in doubt the monophyly of Chrysidoidea and Vespoidea (Pilgrim et al. 2008; Heraty et al. 2011; Johnson et al. 2013; Branstetter et al. 2017; Pauli et al. 2021). The families Dryinidae, Embolemidae and Sclerogibbidae, which form a clade supported by both morphology and molecules (Carpenter, 1986; Brothers and Carpenter 1993; Brothers 2011; Branstetter et al. 2017), have been recovered either as sister group of the Aculeata *s. str.* (Branstetter et al. 2017) or being the sister clade of a group formed by the remaining Chrysidoidea families plus the Aculeata *s.str.* (Pauli et al. 2021). On the other hand, the Vespoidea can be split in at least three lineages, with the Formicidae being consistently recovered as sister group to the Apoidea (Pilgrim et al. 2008; Johnson et al. 2013; Branstetter et al. 2017; Peters et al. 2017).

Incongruence between molecular and morphological hypotheses complicates the assessment of the phylogenetic position of fossil aculeate families in relation to the extant taxa. At present, thirteen fossil families are attributed to Aculeata. Two families from the Cretaceous are recognized in Chrysidoidea: †Chrysobythidae and †Plumalexiidae, both with phylogenetic affinities to the extant families Chrysididae and Plumariidae, respectively (Brothers 2011; Melo and Lucena 2020; Brothers and Melo 2021). Within the Apoidea the fossil families †Allommationidae, †Angarosphecidae, †Cirrosphecidae, and †Spheciellidae, from the Cretaceous, are recognized (Rosa and Melo 2021). The families †Bryopompilidae, †Burmusculidae, †Falsiformicidae, †Holopsenellidae, †Melittosphecidae, and †Panguidae are either tentatively associated to Vespoidea or considered as *incertae sedis* within Aculeata, due to lack of obvious synapomorphies linking them to extant lineages (Rodriguez et al. 2015; Zhang et al. 2018a; Li et al. 2020;

Rasnitsyn et al. 2020; Rosa and Melo 2021; Lepeco and Melo 2022). Finally, the †Bethylonymidae are considered as stem aculeates, with a fossil record dating back to the Middle Jurassic (Rasnitsyn 1975, 1988; Grimaldi and Engel 2005).

Aculeate wasps, including Formicidae, comprise about 61% of all Hymenoptera described from amber deposits in Myanmar, which currently represents the richest source of Cretaceous insects (Rasnitsyn et al. 2016). The fauna found in Burmese amber is remarkable for its endemic aspect, revealing a rich paleoenvironment with no counterparts elsewhere in the globe (Zhang et al. 2018b). Regarding aculeate wasps, eight families are known solely from inclusions in Burmese amber, not being recorded at any other fossil deposit or in the extant fauna. Fossiliferous amber from Myanmar was usually gathered from several mines in the Hukawng Valley, Kachin state, with an estimated age of ca. 99 my (Shi et al. 2012). More recently, other deposits have been explored commercially, including mines in the Sagaing Region, near the township of Hkamti (Liu 2018). Amber from Hkamti is older in relation to Kachin amber, with an estimated age of ca. 110 my (Xing and Qiu 2020).

In the present study, we describe a new family of stinging wasps from the Cretaceous, including three new genera from Burmese amber. We also reinterpret the identity of the fossil genus †*Mirabythus*, described by Cai et al. (2012) based on rock impressions from the Yixian formation, China, and originally attributed to the family Scolebythidae. Key characteristics linking †*Mirabythus* to the newly described family are evidenced.

Methods

The amber pieces containing the new taxa described here were obtained from dealers established in Thailand and China. Pieces are derived from amber mines in northern Myanmar (Hukawng Valley, Kachin state and Hkamti, Sagaing region). A map containing the localities from where the amber was obtained can be found in Xing and Qiu (2020). The examined material, including type specimens, is permanently deposited at the Departamento de Zoologia (DZUP) of the Universidade Federal do Paraná (UFPR) under care of the senior author. In order to have a better view of the inclusions, the pieces were manually trimmed with a jewelry saw and ground with wet emery paper (grit sizes of 800 to 3000). Final polishing was obtained using a sanding sponge pad (grit size of 5000), followed by rubbing in soft cloth.

General morphological terminology mostly follows Huber and Sharkey (1993). The abbreviations F, S and T are employed for flagellomeres, metasomal sterna, and metasomal terga, respectively. We refer to the section of vein Rs enclosing the first submarginal cell as 2Rs. Veins 2r-m and 3r-m are referred to as 2rs-m and 3rs-m respectively. For structures related to the sting apparatus we follow Barbosa et al. (2021), except that the numbering of structures follows the metasomal ordering and not abdominal ordering. Observations and descriptions were made using a Leica M125 stereomicroscope. The color images were obtained by a Leica DFC295 digital camera attached to the stereomicroscope, following the illumination scheme developed by

Kawada and Buffington (2016). The resulting images were merged with the software Zerene Stacker (Zerene Systems, LLC). The figures were enhanced using the free software GIMP 2.8.16 (The GIMP Team). Line drawings of the presently described taxa were made with the aid of a camera lucida. All measurements are given in millimeters (mm). Measurements were taken at an angle that provided the most accurate view of the structure being measured; in the case of body length, when necessary, separate measurements for head, mesosoma and metasoma were summed to provide the total value. Setae were measured relative to the size of the mid ocellus. We used “tiny” for setae shorter than ocellar diameter; “short” for setae not surpassing twice ocellar diameter, “medium-sized” for setae with about 2–3 times ocellar diameter, and “long” for setae surpassing 3 times ocellar diameter. Proportions and measurements of head parts are provided in reference to the anterior-posterior axis.

Results

Systematic paleontology

Hymenoptera Linnaeus, 1758

Apocrita Gerstaecker, 1867

Aculeata Latreille, 1802

†Bethylonymoidea Rasnitsyn, 1975

†Trifionychidae Lepeco & Melo, fam. nov.

<https://zoobank.org/C8401C22-05F8-4797-96FF-B5FE8F1A45F4>

Type genus. †*Trifionyx* Lepeco & Melo, gen. nov.

Included genera. †*Prionaspidion* Lepeco & Melo, gen. nov., †*Trifionyx* Lepeco & Melo, gen. nov., †*Trifionyximus* Lepeco & Melo, gen. nov., †*Mirabythus* Cai, Shih & Ren.

Diagnosis. The following set of characters differentiate †Trifionychidae fam. nov. from other aculeate lineages: falciform mandible, apex abruptly tapering and becoming strongly curved at distal two-thirds; apex of clypeus widely rounded and projecting over mandibles; frons protruding over lateral portion of clypeus, forming tube in which antennal radicle is inserted; antennal socket directed laterally on head, below ocular level; both sexes with nine flagellomeres; partial or complete fusion of veins C and Sc+R on forewing; and base of the metasoma forming small petiole (more easily visualized in ventral view). Other helpful diagnostic characters found in all family members are the percurrent notauli, strongly diverging anteriorly; dorsal surface of propodeum posteriorly delimited by transverse carina; and third valvula very elongated, undivided, and exposed at rest. Additional features unique to some members of the family are the clypeal apex sometimes with serial indentations, giving it a serrate aspect (†*Mirabythus*, †*Prionaspidion* gen. nov. and, to a lesser extent, †*Trifionyx* gen. nov.) and trifid tarsal claws (†*Trifionyx* gen. nov. and †*Trifionyximus* gen. nov.).

Description. *Head.* Large, as wide as or wider than mesosoma; prognathous to obliquely hypognathous. Palps shorter than mandible. Mandible wide basally, with well-delimited depressed region between anterior condyle and posterior acetabulum; distally tapering and curved. Labrum very reduced, inconspicuous. Clypeus large; apex widely rounded and projected over mandibles. Malar space width between one or two times the diameter of scape. Frons protruding over lateral portion of clypeus, forming tube concealing antennal radicle. Compound eye ovoid, bulging. Three ocelli present. Hypostomal bridge long, at least as long as basal mandibular width; anteriorly delimited by strong and curved carina between bases of mandibles. Occipital carina well developed, complete. Antennal socket directed laterally on head, anterior to ocular level; dorsal rim slightly projecting over radicle. *Antenna.* Scape long, tubular, at least twice as long as its maximum width; main shaft of scape forming angle of about 45° in relation to insertion of radicle. Pedicel long, narrowed at base, at least twice as long as its maximum width. Flagellum with nine flagellomeres. *Mesosoma.* Pronotum anteriorly declivitous; pronotal flange well developed, covering propleuron in dorsal view; dorsolateral lobe reaching tegula; posterolateral corner narrow, strongly projecting towards procoxa. Propleuron with percurrent carina dorsally; dorsal and ventral edges completely abutting; posterior edges not diverging; epicoxal lobe present. Basisternum small, most of external portion of prosternum facing backwards. Notaulus well developed, indicated as percurrent sulcus; notauli strongly diverging anteriorly. Parapsidial lines absent. Scutellum shorter than mesoscutum; anteriorly with broad and deep sulcus posterior to transscutal articulation; axillae small. Prepectus absent, mesepisternum forming a continuous sclerite. Ventral portion of mesepisternum anteriorly marked by strong transverse angulation; mesocoxal foramina small, separated from each other by more than twice their width. Metanotum short, not covered by scutellum medially. Metepisternum broadly separating metacoxae ventrally, but not forming plate; submetapleural carina well developed above metacoxa. Metacoxal foramen small. Propodeum long, at least as long as mesoscutum; dorsal and posterior surfaces well defined; spiracle positioned on transition between lateral and dorsal portions of the sclerite; propodeal foramen separated from metacoxal foramina by sclerotized bridge. *Legs.* Coxae small and globose. Femora broad. Protrochanter elongated; inserted posteriorly on procoxa. Meso- and metatrochanters very small, globose. *Forewing.* Veins C and Sc+R partially fused, costal cell obliterated. With one or no submarginal cell enclosed by tubular veins. Veins 3rs-m and 2m-cu absent. Veins not reaching distal margin of wing. *Metasoma.* Basally with small petiole; with seven exposed terga and eight exposed sterna on males; less segments exposed on females. T1 small, forming convex, rounded plate; posterior margin entire; lateral line absent. T2-T6 wider than long, posterior margins widely rounded. S1 rounded, relatively reduced; S2-S5 wider than long, posterior margins widely rounded. Without constriction or specialized articulation between first and second metasomal segments. *Sting apparatus.* Well developed. Seventh sternum enclosing most of sting. Second valvifer very narrow. Third valvula longer than wide, narrow; as a unique piece, without articulation; permanently exposed in some of the taxa. Terebra curving upwards. First and second valvulae of equal size. Furcula well developed, V-shaped, with very short posterior arm.

Key to the genera of †Trifionychidae fam. nov.

- 1 Forewing without cells enclosed by tubular veins, marginal cell absent; head distinctly enlarged, far wider than mesosoma (mid-Cretaceous Burmese amber) **2**
- Forewing with radial and first cubital cells enclosed by tubular veins, marginal cell present, either open or closed; head not distinctly enlarged, slightly wider than mesosoma **3**
- 2 Tarsal claws simple or bifid; eyes glabrous; mesotibia with none or only a single spur; dorsal surface of propodeum without depression between spiracles; lower margin of lateral ocelli well-above upper eye level; disc of clypeus almost flat †*Prionaspidion* Lepeco & Melo, gen. nov.
- Tarsal claws trifid; eyes covered with erect setae; mesotibia with two spurs; dorsal surface of propodeum with transverse depression between spiracles; ocellar triangle below upper eye level; disc of clypeus convex †*Trifionyx* Lepeco & Melo, gen. nov.
- 3 Clypeus well developed, projecting well ahead of mandibular bases, its apex denticulate; submarginal cell relatively short, less than 1.5 times as long as wide, distally closed by vein 2Rs (distal limit of submarginal cell confluent with m-cu); body length above 6 mm (Early Cretaceous of China) †*Mirabythus* Cai et al.
- Clypeus relatively short, slightly projected over mandibular bases, its apex entire, without denticles; submarginal cell relatively long, about twice as long as wide, distally closed by vein 2rs-m, which is distanced from vein m-cu by about its length; body length below 5 mm (mid-Cretaceous Burmese amber) †*Trifionyximus* Lepeco & Melo, gen. nov.

†*Prionaspidion* Lepeco & Melo, gen. nov.

<https://zoobank.org/DB1E645C-2016-4079-A941-20A780DFB298>

Type species. †*Prionaspidion brevidens* Lepeco & Melo, sp. nov.

Included species. †*Prionaspidion brevidens* Lepeco & Melo, sp. nov., †*Prionaspidion nanus* Lepeco & Melo, sp. nov.

Diagnosis. Species in the new genus are characterized by the combination of the following characters: absence of enclosed cells in the forewing; enlarged head, which is far wider than the mesosoma; vertex flat in frontal view; lower margin of lateral ocelli well-above upper eye level; and metasoma shortened, with telescopic segments. Additional diagnostic features are the relatively small eyes in comparison to the head size and the tibial spur formula: 1-1-1 or apparently 1-0-1. Females have simple tarsal claws, while the only known male has bifid claws. In the type species, it seems that the apical portion of the third valvulae is permanently exposed.

Description. Head. Enlarged, far wider than mesosoma; prognathous. Apical margin of clypeus completely filled with indentations or denticles; disc of clypeus about as large as compound eye, almost flat. Frons wider than eye length, flat.

Frontal line indicated as shallow sulcus near mid ocellus. Compound eye relatively small, bulging, glabrous. Vertex flat in frontal view; extending behind lateral ocelli for at least 1.5 times length of ocellar triangle. Lower margin of mid ocellus near upper tangent of compound eye. Lower margin of lateral ocelli well-above upper eye tangent. **Antenna.** F1-F8 about twice as long as maximum width; F1 about as long as F2. **Mesosoma.** Pronotal collar relatively long, at least as long as mesoscutum; anterior surface of pronotum somewhat rounded in dorsal view, with transverse sulcus at mid-height; surface near posterior edge without transverse depression. Surface of mesoscutum between notauli flat, at the same level as lateral surfaces. Mesepisternum with a shallow transverse sulcus above mesepisternal pit. Metanotum with few short carinae on sublateral surfaces. Propodeum with box-like aspect, posterior slope abrupt; dorsal surface not depressed between spiracles. **Legs.** Arolia not enlarged. Tibial spur formula 1-1-1 or apparently 1-0-1. **Forewing.** Without enclosed cell. Veins C and Sc+R completely fused. Pterostigma vestigial. Vein M+Cu nebulous. Vein cu-a absent. Distal portion of vein Cu absent. Vein A spectral. **Hindwing.** Vein C present, nebulous. Vein A absent. **Metasoma.** Short, far shorter than lengths of head and mesosoma combined; segments telescoped within each other.

Etymology. The name is derived from Ancient Greek, being a combination of *prion*, which means “saw”, and *aspidion*, meaning “small shield”, in reference to the clypeus with a series of denticles along its apical margin. It is a neuter name.

†*Prionaspidion brevidens* Lepeco & Melo, sp. nov.

<https://zoobank.org/A83B2DA0-1665-4188-97A4-94D4DBA6FE95>

Fig. 1

Type material. Holotype female in amber piece DZUP Bur-1919. The specimen integument is structurally well preserved, but part of its body was lost due to breaking of the amber piece. The mouthparts are broken; a set of two and another of three palpomeres can be distinguished, but we could not identify if they belong to maxillar or labial palps; the right mandible and the apex of the left one was sanded off. The left antenna is disarticulated, but intact. The right antenna is disarticulated and is represented only by F3 to F9. The right fore and mid legs were sanded off. Parts of the hind wings are present, but we could not identify its shape or venation. The metasoma is compacted, perhaps due to a telescopic capacity of its segments. Syninclusions: the apex of a leaf, which is slightly larger than the specimen; two unidentified mites; stellate trichomes; spores; and debris.

Diagnosis. The species can be separated from †*P. nanus* sp. nov. by the larger body size (over 4 mm); presence of a carina adjacent to inner orbit, reaching dorsal rim of antennal socket (Fig. 1D); denticles on the apical margin of clypeus well defined, at least on sublateral surfaces (Fig. 1C, D); and the relatively slender profemur, about 4.2 times as long as maximum width.

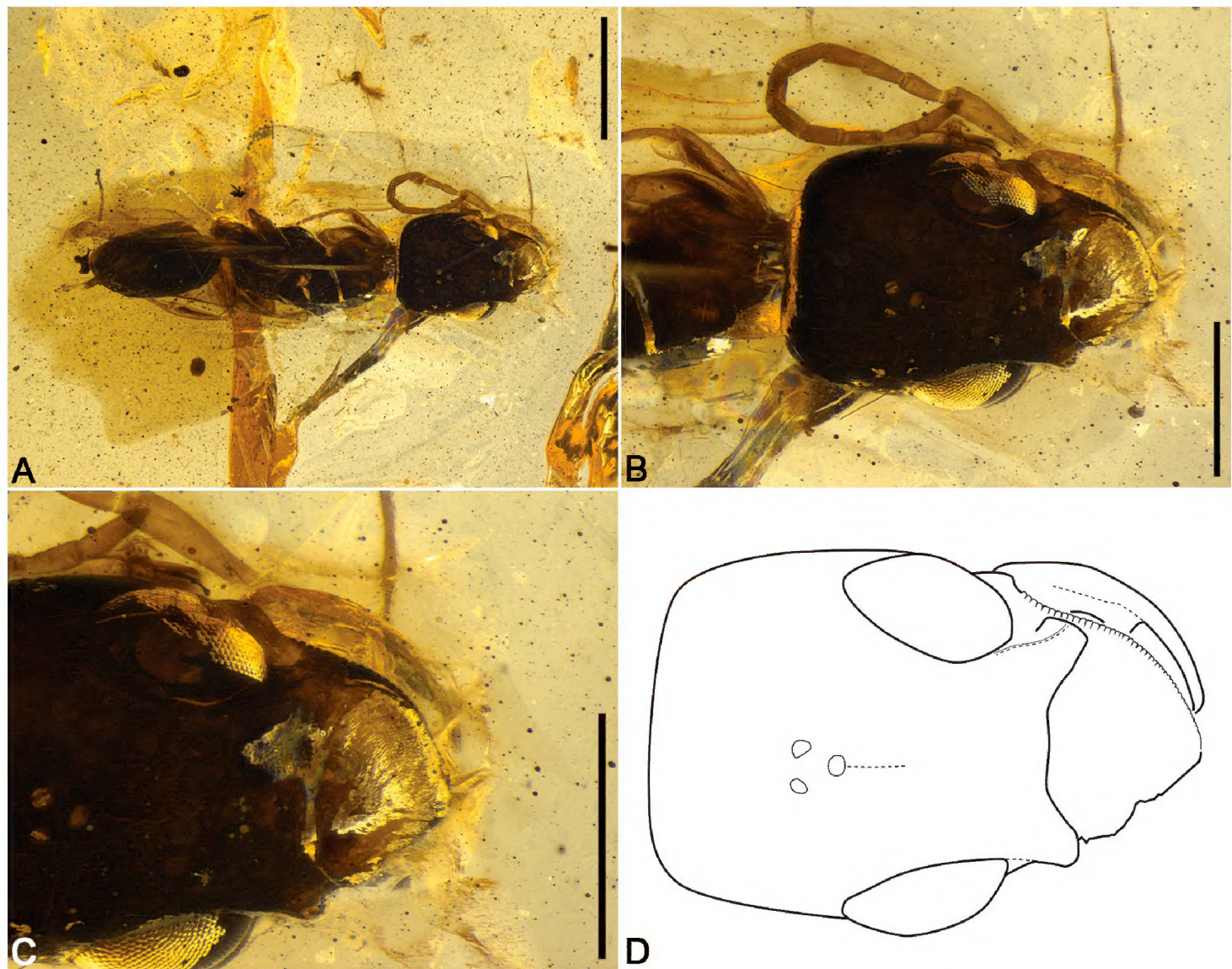


Figure 1. Holotype female of †*Prionaspidion brevidens* sp. nov. (DZUP Bur-1919) **A** habitus, dorsal view **B** dorsal view of head **C** close-up of clypeus. Scale bar: 0.5 mm. **D** line drawing of head, dorsal view, not in scale. Scale bar: 1mm (**A**); 0.5 mm (**B, C**).

Description. Female. Measurements: approximate body length: 4.2 mm; maximum head length: 1.1 mm; maximum head width: 0.9 mm; medial clypeus length: 0.3 mm; approximate forewing length: 2.0 mm. **Color.** Poorly preserved, body apparently brown. Wings hyaline, veins light brownish. **Pubescence.** Head, metasoma and most of mesosoma apparently glabrous. Mesepisternum with sparse coverage of tiny setae on lateral surface. Short bristles visible on apex of tarsomeres; first tarsomere of all legs densely covered by small setae. Forewing with homogeneous coverage of tiny setae; anterior margin with dense tiny setae, setae as long as half width of vein C+Sc+R. **Sculpturing.** Smooth overall. Head apparently with tiny scattered punctures. Lateral portion of mesepisternum with sparse punctures. Metapostnotum filled with rugae delimiting wide spaces; medially with a straight longitudinal carina; dorsal surface of propodeum rugose posteriorly. **Structure.** Palps not distinguishable. Clypeal disc about twice as wide as long, larger than compound eye; apical margin with homogeneously sized, deep, blunt indentations. Frons with strong carina adjacent to inner orbit and reaching dorsal rim of antennal socket. Eyes separated medially by about 1.4 times eye length. Mid ocellus separated from lateral ocellus by about its diameter. Lateral

ocellus distanced from inner orbit of eye by about 2.5 times ocellar triangle length. Vertex extending behind lateral ocelli for about twice the length of ocellar triangle. Hypostomal bridge as long as 1.5 times basal mandibular width. Scape about 4 times as long as maximum width; pedicel about as long as F1. Metapostnotum visible externally, occupying most of the dorsal surface of propodeum medially. Profemur about 4.2 times as long as maximum width. Basitarsomere of fore leg as long as 0.7 times protibial length. Tibial spur formula apparently 1-0-1. Basitarsomere of hind leg about 0.6 times metatibial length. Tarsal claws simple.

Etymology. The name is a combination of the Latin *brevis*, meaning “short”, and *dens*, meaning “tooth”. The name is an allusion to the presence of a series of short denticles on the clypeal margin. It is a noun in apposition.

†*Prionaspidion nanus* Lepeco & Melo, sp. nov.

<https://zoobank.org/29966B39-4973-40C8-9471-66D79BB77EBE>

Figs 2–4

Type material. Holotype male in amber piece DZUP Bur-2265 (Fig. 2). The specimen is almost fully articulated, except for part of the right metatarsus, and a detached metasomal sclerite, near the metasoma. Syninclusions: an unidentified mite and a large number of debris and plant trichomes. Paratype specimen (apparently a female, judging by the simple tarsal claws) in amber piece DZUP Bur-1127 (Figs 3, 4). The specimen is relatively well preserved, fully articulated, with the exception of the distal portion of the metasoma and the hind wings. No sting or genitalia are present on the piece. A bubble hinders the visualization of the propodeum. Syninclusions: five unidentified mites and debris.

Diagnosis. The species can be separated from †*P. brevidens* sp. nov. by the smaller body size (forewing length between 1.3 and 1.4 mm in the examined specimens); carina on the dorsal rim of antennal socket not reaching the inner orbit; poorly defined and irregularly sized denticles on the apical margin of clypeus; and the relatively robust profemur, about 2.5 times as long as maximum width.

Description. Holotype male. Measurements. Approximate body length: 2.3 mm; maximum head length: 0.7 mm; maximum head width: 0.5 mm; medial clypeus length: 0.2 mm; approximate forewing length: 1.4 mm. **Color.** Poorly preserved, body apparently dark brown. Legs yellowish. Wings hyaline, veins light brownish. **Pubescence.** Head mostly glabrous, except for short erect setae on mandible and clypeus. Mesosoma and most of metasoma apparently glabrous. Legs mostly with short setae; apex of tarsomeres with two to five short bristles. Apex of T4 and T5 with sparse long setae. Forewing with homogeneous coverage of tiny setae; anterior margin with dense tiny setae, setae as long as half width of vein C+Sc+R. **Sculpturing.** Smooth, where preserved. Metapostnotum apparently occupying most of dorsal surface of propodeum medially, without basal rugae. **Structure.** Maxillary palp with at least three palpomeres. Labial palpomeres not distinguishable. Mandible tridentate, upper tooth larger than lower teeth. Clypeal disc

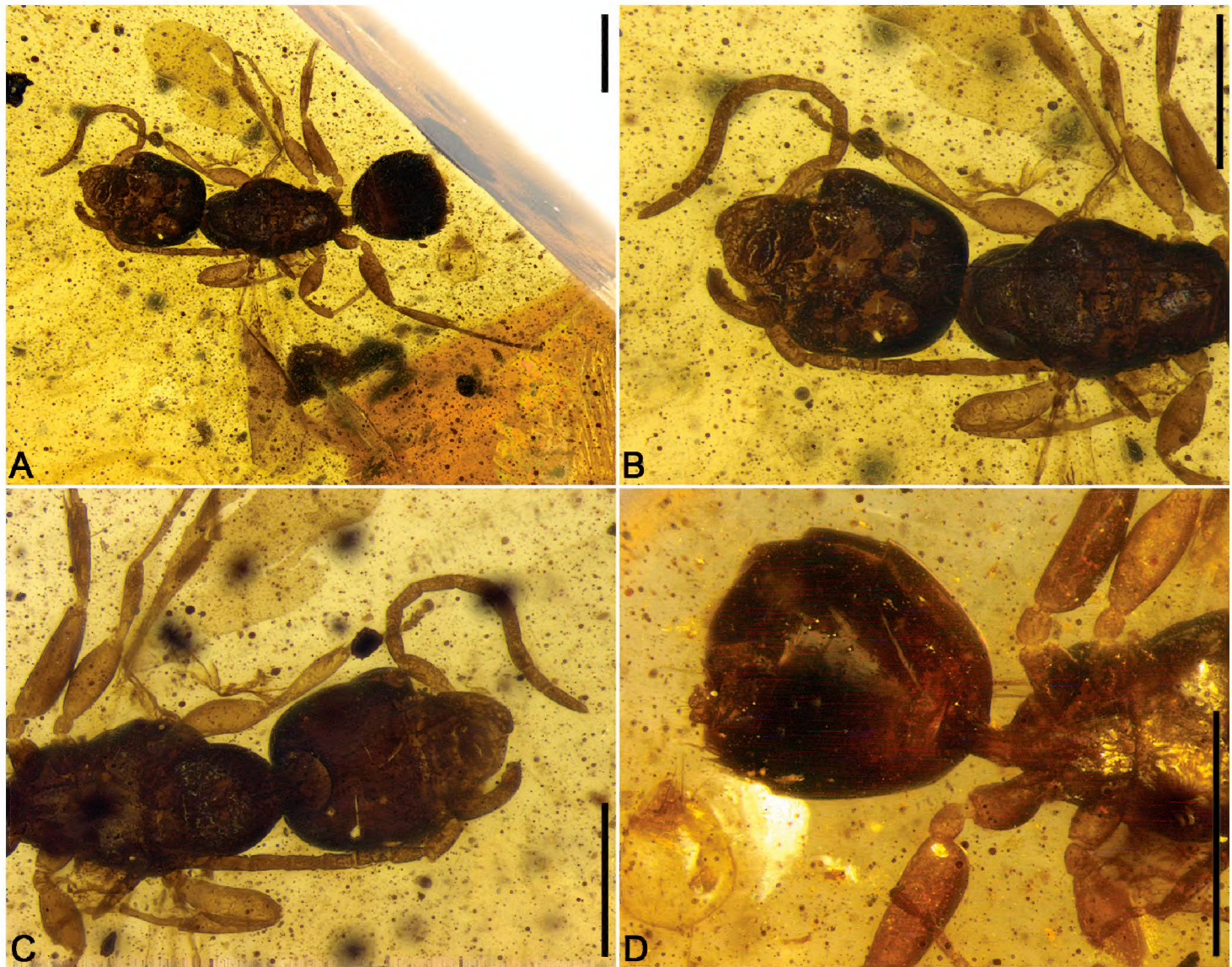


Figure 2. Holotype male of †*Prionaspidion nanus* sp. nov. (DZUP Bur-2265) **A** habitus, dorsal view **B** dorsal view of head and mesosoma **C** ventral view of head and mesosoma **D** ventral view of metasoma. Scale bars: 0.5 mm.

about as wide as long, slightly smaller than compound eye; apical margin with irregular, weak, blunt denticles. Frons without strong carina adjacent to inner orbit; dorsal rim of antennal socket with low carina directed towards frons. Eyes separated medially by about eye length; lower orbits slightly converging. Mid ocellus separated from lateral ocelli by about 1.5 times its diameter. Lateral ocellus separated from inner orbit of eye by about 3 times ocellar triangle length. Vertex extending behind lateral ocelli for about 1.5 times the length of ocellar triangle. Hypostomal bridge 3.5 times as long as basal mandibular width. Scape about 4 times as long as maximum width; pedicel about 1.3 times as long as F1. Profemur about 2.5 times as long as maximum width. Basitarsomere of fore leg as long as 0.5 times protibial length. Tibial spur formula 1-1-1. Basitarsomere of hind leg about as long as 0.7 times metatibial length. Tarsal claws bifid.

Paratype female. As for the male, except: **Measurements.** Approximate body length: 2.0 mm; maximum head length: 0.6 mm; maximum head width: 0.5 mm; medial clypeus length: 0.1 mm; approximate forewing length: 1.3 mm. **Color.** Poorly preserved, body apparently brown. **Pubescence.** Head, mesosoma and most of metasoma

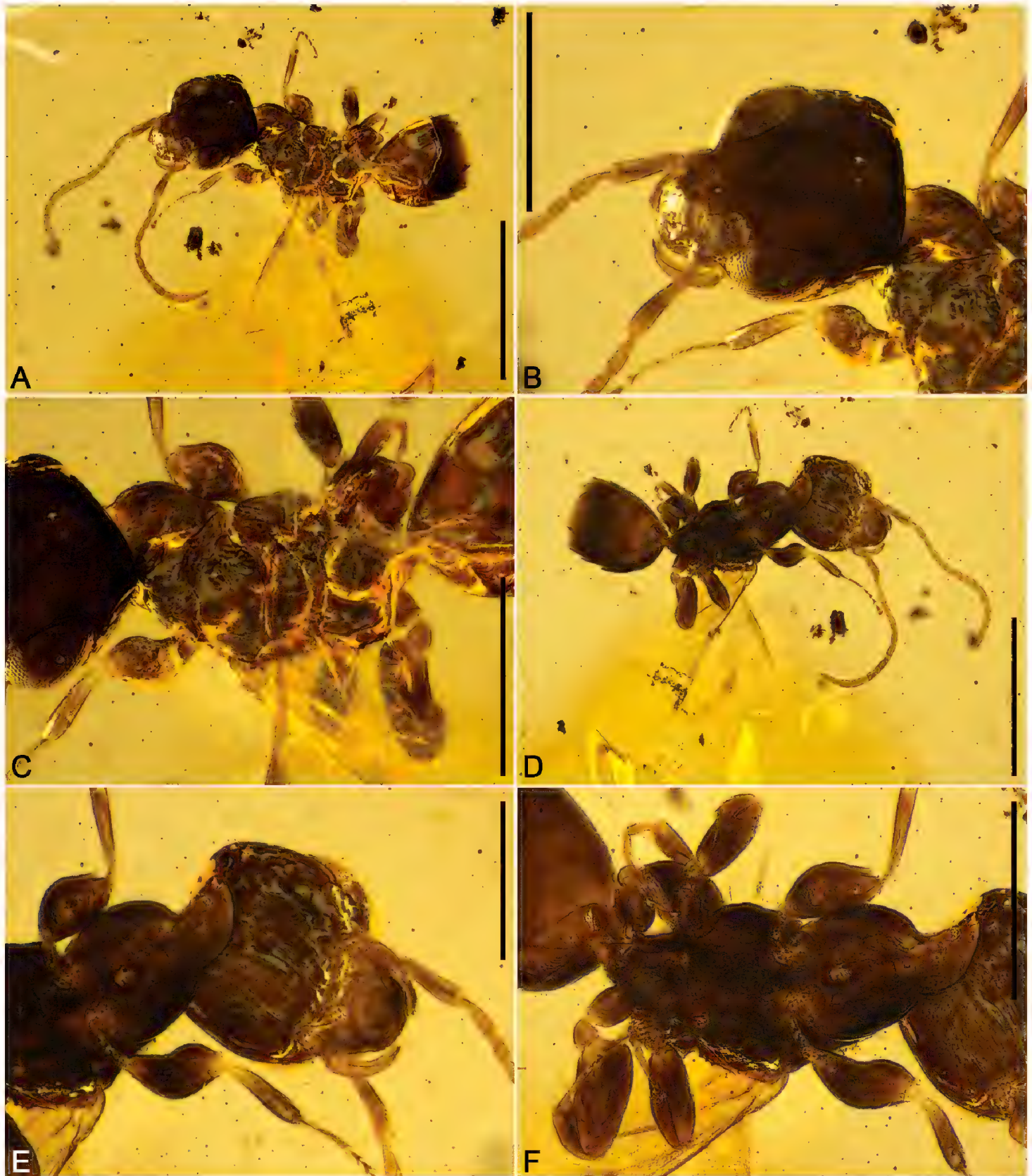


Figure 3. Paratype (apparently female) of †*Prionaspidion nanus* sp. nov. (DZUP Bur-1127) **A** habitus, dorsal view **B** head, dorsal view **C** mesosoma, dorsal view **D** habitus, ventral view **E** head, ventral view **F** mesosoma, ventral view. Scale bar: 1 mm (**A, D**); 0.5 mm (**B, C, E, F**).

apparently glabrous. Apex of T4 and T5 with sparse setae. **Sculpturing.** Head apparently with tiny scattered punctures. **Structure.** Head slightly shorter than that of male; tibial spur formula apparently 1-0-1; tarsal claws simple.

Etymology. The name is derived from the Latin *nanus*, meaning “dwarf”, in allusion to the relatively small size of the species. The name is an adjective.



Figure 4. Paratype (apparently female) of †*Prionaspidion nanus* sp. nov. (DZUP Bur-1127). Habitus, ventral view. Scale bar: 1 mm.

†*Trifionyx* Lepeco & Melo, gen. nov.

<https://zoobank.org/C7CFFCD0-D5DF-43EF-9514-E5A12EFADBA5>

Type species. †*Trifionyx pilosus* Lepeco & Melo, sp. nov.

Diagnosis. The single species allocated in this genus is differentiated from †*Mirabythus* and †*Trifionyximus* gen. nov. by the absence of cells enclosed by tubular veins in the forewing (Fig. 5F) and the enlarged head, which is far wider than mesosoma. From †*Prionaspidion* gen. nov. it can be differentiated by the trifid tarsal claws (Fig. 5G); tibial spur formula 1-2-2; dorsal surface of propodeum with a transverse depression between spiracles (which may correspond to the metapostnotum); ocellar triangle below upper eye level and convex clypeus disc. †*Trifionyx* gen. nov. is unique within †Trifionychidae fam. nov. in having the body with conspicuously developed pubescence, including on the compound eyes.

Description. Head. Enlarged, far wider than mesosoma; prognathous. Entire apical margin of clypeus with small denticles; disc of clypeus relatively large, convex. Frons wider than twice eye length, flat. Frontal line not indicated. Compound eye relatively small, bulging, covered with erect setae. Vertex arcuate in frontal view; extending behind lateral ocelli for at least 1.5 times length of ocellar triangle. Mid ocellus

far below upper tangent of compound eye. Lower margin of lateral ocelli below upper eye tangent. **Antenna.** F1 3 times as long as maximum width, longer than F2; F2–F8 about twice as long as maximum width. **Mesosoma.** Pronotal collar relatively short, as long as half-length of mesoscutum; anterior surface of pronotum somewhat rounded in dorsal view, with transverse sulcus at mid-height; surface near posterior edge with transverse depression. Surface of mesoscutum between notauli slightly convex, level with lateral surfaces. Mesepisternum with a shallow transverse sulcus above mesepisternal pit. Metanotum with few short carinae on sublateral surfaces. Propodeum without box-like aspect, posterior slope convex; dorsal surface depressed transversally between spiracles. **Legs.** Arolia not enlarged. **Forewing.** Veins C and Sc+R completely fused. Pterostigma present. Marginal cell absent. Submarginal cell not enclosed by tubular veins. Radial, first cubital, and medial cells defined by nebulous veins. Vein M+Cu nebulous. Vein cu-a nebulous. Distal portion of vein Cu nebulous. Vein A spectral. **Hindwing.** Vein C present, nebulous. Vein A absent. **Metasoma.** Apparently short, shorter than mesosoma; segments apparently not telescoped within one another.

Etymology. The name is derived from Latin and results from the combination of *trifidus*, meaning “cleft into three”, and *onyx*, meaning “claw”. The name is masculine.

† *Trifionyx pilosus* Lepeco & Melo, sp. nov.

<https://zoobank.org/CD33CC38-52EE-43F2-99CE-9144030EF0A5>

Fig. 5

Type material. Holotype female in amber piece DZUP Bur-1906. The specimen is fully articulated, but part of the left fore leg, apex of forewings, and part of metasoma were sanded off. As the metasoma is curved frontwards, it retains part of the sting apparatus. There are no visible syninclusions.

Diagnosis. As for the genus.

Description. Holotype female. Measurements: approximate body length: 4.5 mm; maximum head length: 0.9 mm; maximum head width: 1.1 mm; medial clypeus length: 0.2 mm; approximate forewing length: 2.2 mm. **Color.** Poorly preserved, apparently dark brown. Apical margin of clypeus darkened, apparently black. Wings hyaline, veins brown. **Pubescence.** Head mostly covered with medium-sized setae, except for frons and vertex, apparently glabrous. Setae on hypostomal bridge relatively longer. Antenna densely covered with tiny decumbent setae. Mesosoma mostly with sparse medium-sized setae. Legs mostly covered by short setae; femora with longer setae on inner surface. Forewing with homogeneous coverage of tiny setae; anterior margin with dense tiny setae, setae as long as one-half C+Sc+R width. Apex of metasoma with very long erect setae. **Sculpturing.** Smooth, where preserved. **Structure.** Maxillary palp with five palpomeres. Labial palp slightly shorter than maxillary palp, apparently with four palpomeres. Mandible simple, without preapical teeth. Clypeus disc wider than medial length, slightly larger than compound eye; denticles on apical margin barely distinguishable. Frons without carina adjacent to inner orbit; dorsal rim of antennal socket with slight carina directed towards frons. Mid ocellus

separated from lateral ocelli by about twice its diameter. Lateral ocellus distanced from inner orbit of eye by about 1.5 times ocellar triangle length. Vertex extending behind lateral ocelli for about 1.5 times ocellar triangle. Hypostomal bridge 3 times as long as basal mandibular width. Scape about 3 times as long as maximum width; pedicel less than 0.5 times as long as F1. Metapostnotum not indicated by sculpturation externally. Profemur about 2.7 times as long as maximum width. Tibial spur formula 1-2-2. Basitarsomere of fore leg as long as 0.8 times protibial length. Basitarsomere of hind leg about as long as 0.8 times metatibial length. Tarsal claws trid.

Etymology. The specific epithet means “pilose”, in allusion to the abundant pilosity of the type species. The name is an adjective.

† *Trifionyximus* Lepeco & Melo, gen. nov.

<https://zoobank.org/B883DD04-525B-4FC8-9995-32AA463818A4>

Type species. † *Trifionyximus cracens* Lepeco & Melo, sp. nov.

Diagnosis. The new genus is distinguished from the other genera described from Burmese amber by the presence of enclosed cells in the forewing (Fig. 6E); and head comparatively small. From † *Mirabythus*, it differs in having the clypeus relatively short with a smooth apex, without denticles; and submarginal cell relatively long, about twice as long as wide, distally closed by vein 2rs-m (in † *Mirabythus* the cell is closed distally by vein 2Rs, judging by its confluence with m-cu), which is distanced from vein m-cu by about its length. An additional difference between both genera is the smaller size of † *Trifionyximus* gen. nov., not surpassing 5 mm.

Description. Head. Not enlarged, slightly wider than mesosoma; obliquely hypognathous. Apical margin of clypeus entire, without denticles; disc of clypeus smaller than compound eye, strongly convex. Frons gently convex. Frontal line inconspicuous. Compound eye relatively large, occupying most of lateral surface of head, glabrous. Vertex arcuate, short, extending behind lateral ocelli for less than length of ocellar triangle. Lower margin of lateral ocelli below upper eye tangent. **Antenna.** F1–F8 about 1.5 times as long as maximum width; F1 about as long as F2. **Mesosoma.** Pronotal collar longer than mesoscutum; anterior surface somewhat narrowed medially in dorsal view, with transverse sulcus at mid-height; surface near posterior edge depressed transversally. Surface of mesoscutum between notauli convex, bulging in relation to lateral surfaces. Mesepisternum without transverse sulcus above mesepisternal pit. Metanotum without carinae on sublateral surfaces. Propodeum without box-like aspect, posterior slope convex; dorsal surface not depressed between spiracles. **Legs.** Arolia enlarged. **Forewing.** Veins C and Sc+R partially fused. Vein C nebulous, costal cell very narrowed and obscured at its mid-length. Pterostigma well developed, small. Marginal cell open, distal portion of vein Rs ending as nebulous vein near distal margin of wing. Submarginal cell posteriorly closed by 2rs-m. Medial cell posteriorly closed by nebulous veins. Vein M+Cu tubular. Vein cu-a tubular. Distal portion of vein Cu ending as a nebulous vein near distal margin of wing. Vein A tubular. **Hindwing.** Vein C present, tubular for at least basal third of wing, becoming nebulous distally. Vein A present,

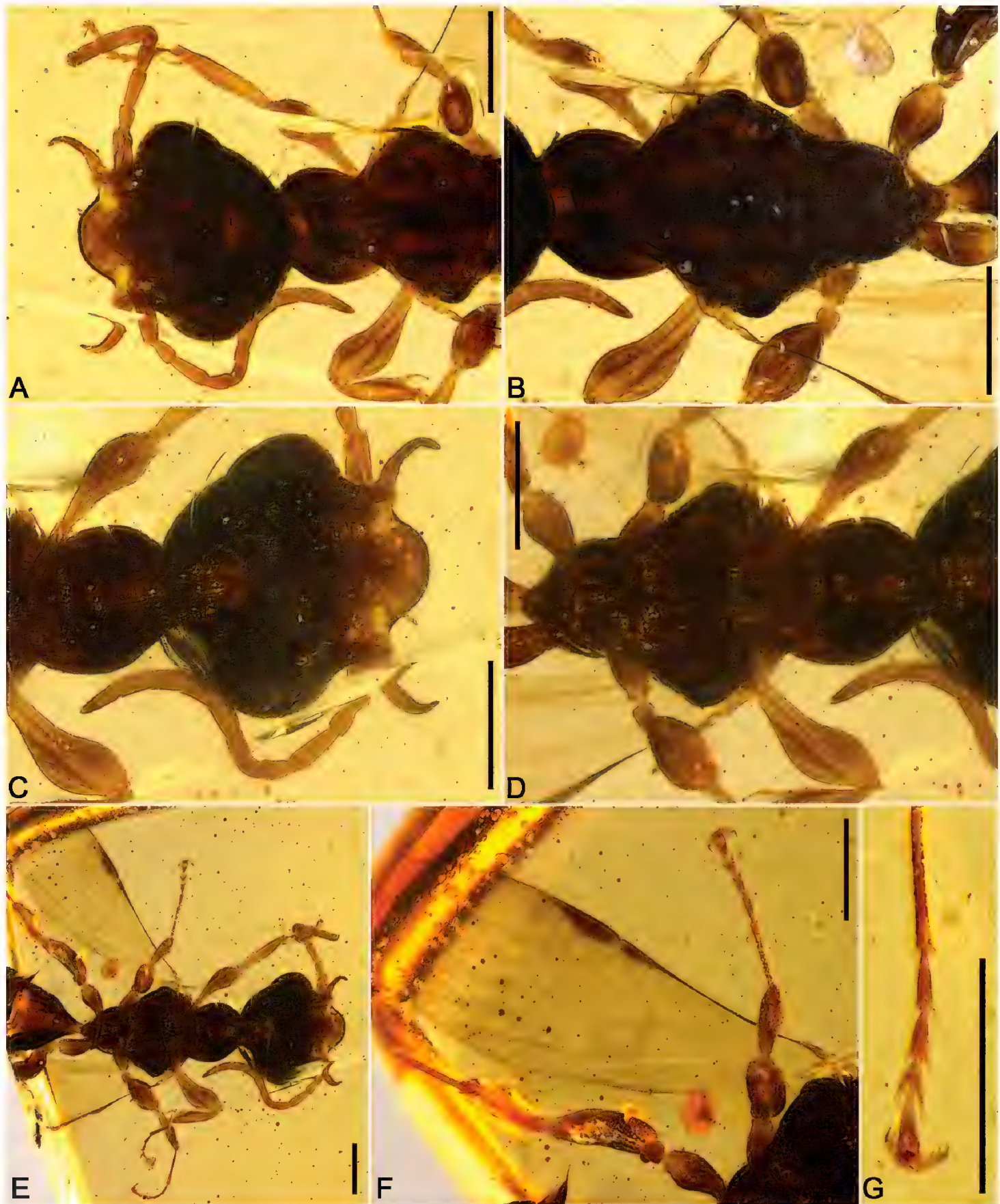


Figure 5. †*Trifionyx pilosus* sp. nov. Holotype female (DZUP Bur-1906) **A** dorsal view of head and mesosoma **B** dorsal view of mesosoma **C** ventral view of head **D** ventral view of mesosoma, habitus, ventral view **E** wings **F** detail of mesotarsal claw. Scale bars: 0.5 mm.

short. **Metasoma.** Long, but shorter than lengths of head and mesosoma combined; segments not distinctly telescopic within each other.

Etymology. The name is derived from the type genus of the family with the addition of the Latin suffix *-imus*, meaning “pertaining to” or “related to”. The name is masculine.

†*Trifionyximus cracens* Lepeco & Melo, sp. nov.

<https://zoobank.org/EE0362A0-0A7F-43CD-B84C-475AB469BA66>

Fig. 6

Type material. Holotype female in amber piece DZUP Bur-828. The specimen is fully articulated, but part of the right antenna was sanded off. The right forewing apex is fragmented. The left side of the head, the posterior portion of the mesosoma and parts of the metasoma are covered by calcite. There are no syninclusions except for scattered debris. The paratype male is in amber piece DZUP Bur-1386. The specimen is fully articulated, but parts of the mesosoma and the legs are diaphanized. Part of the right antenna was sanded off during preparation. A large calcite bubble obstructs the view of part of the left side of the mesosoma. Syninclusions: a small psocid.

Diagnosis. As for the genus.

Description. Female Holotype. Measurements: approximate body length: 3.6 mm; maximum head length: 0.7 mm; approximate forewing length: 1.9 mm. **Color.** Poorly preserved, apparently dark brown. Wings hyaline, veins brown. **Pubescence.** Head sparsely covered with short setae. Forewing with homogeneous coverage of tiny setae; anterior margin with dense tiny setae, setae as long as half width of veins C+Sc+R. **Sculpturing.** Smooth, where preserved. **Structure.** Maxillary palp with at least three palpomeres. Labial palp not distinguishable. Mandible quadridentate, with three preapical teeth with similar sizes, lower tooth larger than preapical teeth. Clypeus disc about as wide as long, far smaller than compound eye. Frons without carina adjacent to inner orbit; dorsal rim of antennal socket without carina directed towards frons. Mid ocellus separated from lateral ocelli by about its diameter. Lateral ocellus distanced from inner orbit of eye by about ocellar triangle length. Vertex extending behind lateral ocelli for about the width of mid ocellus. Hypostomal bridge 3 times as long as basal mandibular width. Scape about twice as long as maximum width; pedicel about 1.5 times as long as F1. Metapostnotum obstructed. Profemur about 1.2 times as long as maximum width. Tibial spur formula 1-2-2. Basitarsomere of fore leg as long as 0.5 times protibial length. Basitarsomere of hind leg about as long as 0.7 times metatibial length. Tarsal claws trid.

Male Paratype. As for the female, except: **Measurements:** approximate body length: 3.0 mm; maximum head length: 0.5 mm; maximum head width: 0.6 mm; medial clypeus length: 0.1 mm; approximate forewing length: 1.8 mm. **Color.** Head black. Color not preserved in legs and mesosoma, due to diaphanization. Metasomal sclerites apparently dark brown. Wings hyaline, slightly darkened near marginal cell, veins dark brown. **Pubescence.** Head, mesosoma and most of metasoma apparently glabrous. Apical metasomal sclerites with sparse erect setae. **Sculpturing.** Smooth, where preserved. **Structure.** Upper tooth of mandible smaller than lower tooth. Scape about 3 times as long as maximum width. Profemur about twice as long as maximum width.

Etymology. From the Latin *cracens*, meaning “slender”, in allusion to the body shape of the type specimens. The name is an adjective.



Figure 6. †*Trifionyxis cracens* sp. nov. **A, B** holotype female (DZUP Bur-828) **A** habitus, dorsolateral view **B** dorsolateral view of head and mesosoma **C–F** paratype male (DZUP Bur-1386) **C** habitus, lateral view **D** head, lateral view **E** forewing. Scale bar: 1 mm (**A, C**); 0.5 mm (**B**); 0.2 mm (**D**); 0.4 mm (**E**).

†*Trifionychidae* sp. indet.

Fig. 7

Comments. We refer here to a female belonging to †*Trifionychidae* fam. nov., found in amber piece DZUP Bur-332 and represented by the head, most of the mesosoma and fragments of the metasoma. The female is clearly a representative of the new family due to the presence of nine flagellomeres; characteristically curved mandibles; frons protruding over lateral portions of clypeus; and trifid tarsal claws. The specimen is interesting for the presence of a dissected sting apparatus and for having the head plus

the propleura and fore legs detached from the remainder of the body. The parts are very close to the body, and are congruent to what is found in other representatives of the family. The anterior portion of its mesopleura can be observed without obstruction and it is possible to see that it lacks a prepectus. The whole region forms an entire sclerite without any indication of articulation or line of fusion of the prepectus with the mesopleura. In relation to the sting apparatus, although most of the sclerites associated to the sting are lost or scattered through the piece, the characteristic upward curvature of the sting shaft can be visualized (Fig. 7D). We opted to not describe this inclusion as a new taxon or assign it to any species of †Trifionychidae fam. nov., due to the absence of forewings, which are essential to differentiate genera within the family. Nevertheless, the specimen seems to be more related to †*Tryfionyximus* gen. nov., due to the relatively small clypeus, trifid claws and the propodeum lacking a box-shape aspect and without transverse depression between spiracles.

†*Mirabythus* Cai, Shih & Ren

Figs 8, Suppl. material 1: figs S1–S5

†*Mirabythus* Cai, Shih & Ren, 2012 in Cai et al. (2012): 58. Type species: †*Mirabythus lechrius* Cai, Shih & Ren, 2012.

Comments. In the original description, Cai et al. (2012) considered that the mandibles of †*Mirabythus* had a series of small notches on the anterior surface. We interpret that these notches correspond in fact to the apical margin of the clypeus, a condition also found in †*Prionaspidion* gen. nov. and †*Trifionyx* gen. nov. (more evident in †*P. brevidens* sp. nov.). The clypeus of †*Mirabythus* is large, comprising nearly one-third of the entire head length, as indicated by the position of the epistomal groove (Fig. 8C, D). The apical margin of the clypeus and the anterior surface of the mandibles are aligned in the type specimens, and this is also observed in specimens from Burmese amber. The antennal sockets of †*Mirabythus* are directed towards the apical margin of the clypeus, below the lower eye tangent (Fig. 8C, D). Cai et al. (2012) represent with dashed lines at least fourteen articles in the antennae of †*M. liae*. For us, it is nearly impossible to count the number of antennomeres in the holotype. In the case of †*M. lechrius*, we can clearly see nine flagellomeres in the holotype, with the first two being far longer than the remaining flagellomeres (Fig. 8A, B).

It is difficult to determine whether the anterior flange of the pronotum is well developed, but none of the specimens exhibit a long propleura with a wide membranous area medially, as is found in most Scolebythidae. We interpret that the propleura are covered in dorsal view and, therefore, the pronotal flange is present. In both type specimens the legs are curled below the body, hindering the interpretation of structures in the ventral surface of the mesosoma, but two main characteristics can be observed. First, the structure originally interpreted as a large prosternum seems to

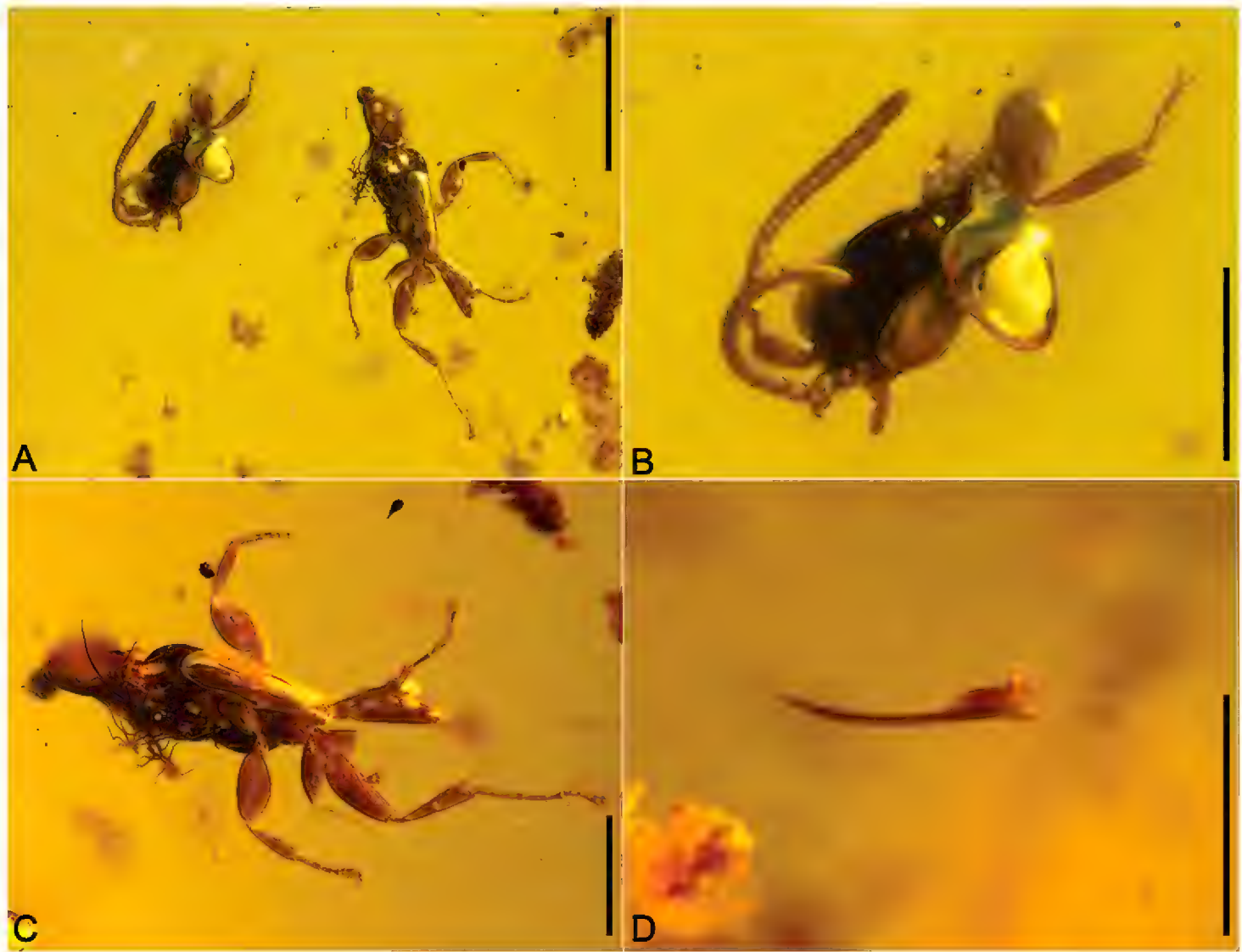


Figure 7. †*Trifionyichidae* sp. indet. (DZUP Bur-332) **A** general view of head and mesosoma **B** head, dorsal view **C** mesosoma, ventral view **D** detail of sting. Scale bar: 1 mm (**A**); 0.5 mm (**B–D**).

represent a void area, where the anterior portion of the mesosoma has detached from the mesepisternum (Fig. 8A, B). In †*M. liae* this detachment is more evident than in †*M. lechrius*. We interpret that the basisternum (the ventrally exposed portion of the prosternum) is not as large as in scolebythids, for both species, similar to what is observed in †*Prionaspidion nanus* sp. nov. Second, a transverse dark line can be seen crossing the mesepisternum of both type specimens (more conspicuous in †*M. liae*), which probably represents the angulation of the mesepisternum found in Burmese amber trifionyichids (Fig. 8A, B). This angulation is not found in *Scolebythidae*. The propodeum has a transverse angulation marking its posterior declivity in both specimens, a characteristic found in the new family, but not in *Scolebythidae*. The point of insertion of the trochanters on the procoxae is difficult to interpret in both specimens, but it is clearly not basal as in all *Scolebythidae*. At least one tibial spur is visible in the hind leg of the holotype of †*M. lechrius*. In none of the specimens of †*Mirabythus* it is possible to identify a costal cell on the forewing, and we interpret that, as in the species from Burmese amber, the veins C and Sc+R are fused along most of the anterior margin of the wing (Fig. 8A, B).

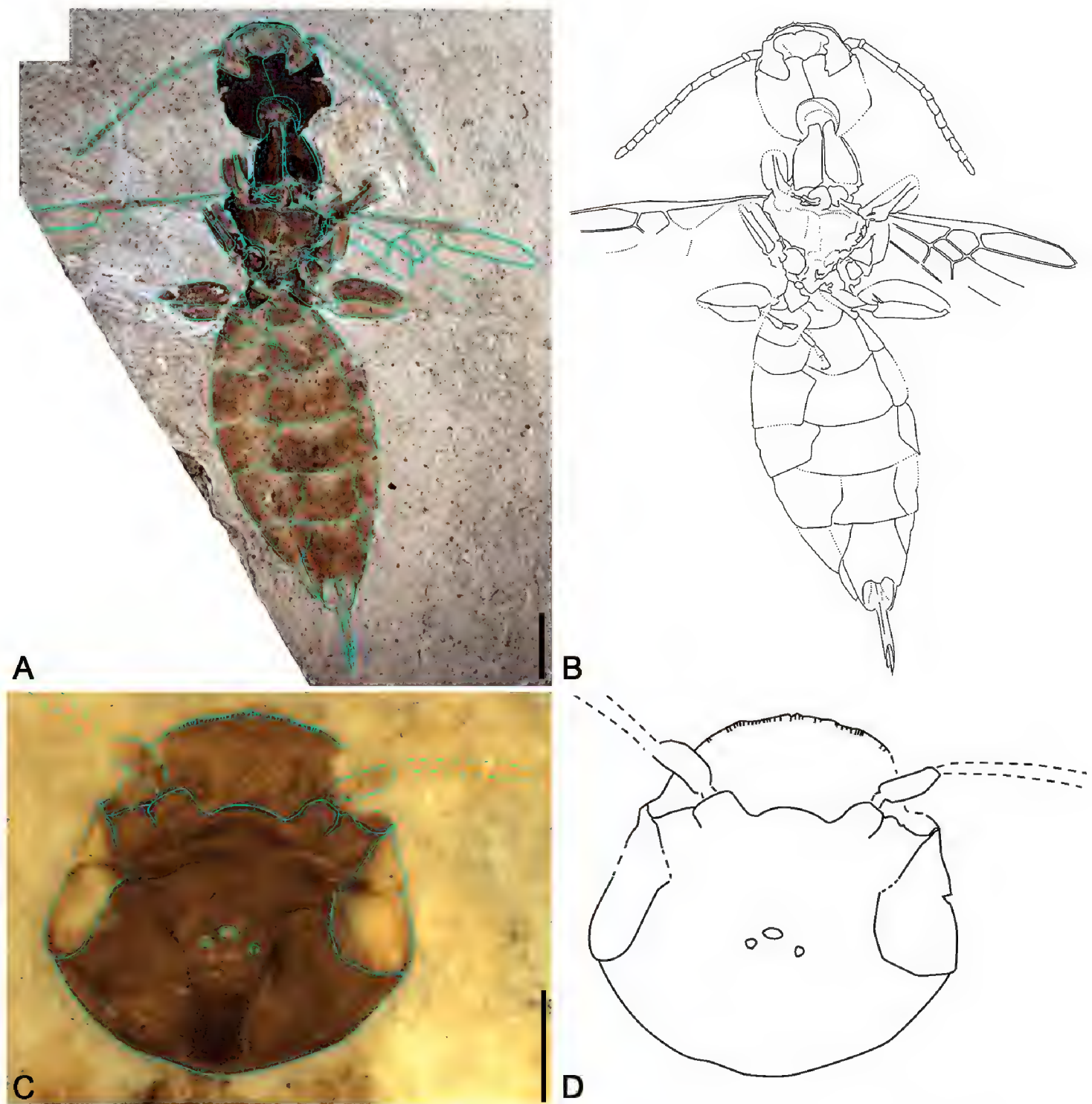


Figure 8. †*Mirabythus* Cai et al. **A, B** †*Mirabythus lechrius* Cai et al. 2012 **A** photograph of habitus, ventral view, line drawing superimposed **B** habitus, ventral view, line drawing isolated **C, D** †*Mirabythus liae* Cai et al. 2012 **C** photograph of head, dorsal view, line drawing superimposed **D** head, dorsal view, line drawings isolated. Photograph credits: Taiping Gao and Yaping Cai. Scale bar: 2 mm (**A, B**); 1 mm (**C, D**).

Part of the sting apparatus is evident in both specimens, including most of the third valvula, which is unsegmented and apparently has its apical portion permanently exposed. The terebra in the holotype of †*M. lechrius* also apparently curves upward, as in other †Trifionychidae fam. nov. In Scolebythidae the terebra is curved downward. The third valvula and terebra of †*Mirabythus* are distinctly elongated, relatively longer in comparison to females of Scolebythidae and other chrysidoids. The two unidentified specimens illustrated by Cai et al. as †*Mirabythus* *indet* are putative members of †Trifionychidae gen. nov. as well, although many characters are not clearly visible. Additional figures of †*M. lechrius* and †*M. liae* are available at Suppl. material 1: figs S1–S5.

Discussion

The new taxa described herein add to the pool of fossil lineages of aculeate wasps and improve our understanding about the Cretaceous entomofauna. Based on these species and on the reinterpretation of †*Mirabythus*, the novel family comprises at least four distinct genera and six species described, indicating that †Trifionychidae fam. nov. were a prolific lineage that thrived at least in the eastern landmasses of the globe during the first-half of the Cretaceous period. Unfortunately, no putative members of the family have been found in other fossil deposits besides the Burmese amber and the Yixian formation, limiting the amount of information we have about this lineage.

The two species of the genus †*Mirabythus* were misinterpreted as scolebythid wasps, but undoubtedly belong in †Trifionychidae fam. nov. Placement of the genus within the new family is supported by the characteristic curvature and tapering of the mandible; the large clypeus with a series of denticles on the apical margin (as in species of †*Prionaspidion* gen. nov. and †*Trifionyx* gen. nov.); the frons protruding over lateral portions of clypeus, directing the antennal sockets downwards below ocular level; and the presence of nine flagellomeres. The reinterpretation of †*Mirabythus* narrows the fossil record of Scolebythidae in the Early Cretaceous to three species from the Barremian, described from inclusions in Lebanese amber (Prentice et al. 1996; Engel and Grimaldi 2007). Concomitantly, the fossil record of Scolebythidae is now represented only by amber inclusions, since †*Mirabythus* was the only taxon attributed to the family with representatives preserved as rock impressions.

At the present moment, it is not possible to indicate with certainty the phylogenetic placement of †Trifionychidae fam. nov. The presence of an equal number of flagellomeres in both sexes, seven exposed metasomal terga and lack of specialized articulation or constriction between the first two metasomal segments rule out the positioning of the family among lineages of Aculeata *s. str.* (see Brothers 1975; Brothers and Carpenter 1993). In addition, members of the new family do not resemble any extant or extinct group belonging to Aculeata *s. str.* Even so, the similarity with Chrysidoidea is derived from a combination of plesiomorphic and independently acquired apomorphic characters, and the new family also does not exhibit obvious synapomorphies relating it to families within Chrysidoidea.

The flagellum with nine articles is an unusual feature among Chrysidoidea. All representatives of Scolebythidae, †Plumalexiidae and †Chrysobythidae, as well as most species of Bethyidae, Chrysididae and Plumariidae have antennae with eleven flagellomeres (Finnamore and Brothers 1993; Melo and Lucena 2020; Brothers and Melo 2021; Lepeco and Melo, unpublished data), with reductions to ten or eight flagellomeres occurring in rather derived lineages (Brothers 1975; Azevedo et al. 2018; Lucena and Almeida 2022). On the other hand, Dryinidae and Embolemidae usually have eight flagellomeres, while Sclerogibbidae may exhibit a multiarticulate flagellum, with at least twelve flagellomeres (Finnamore and Brothers 1993; Perkovsky et al. 2020). Therefore, the number of flagellomeres does not link †Trifionychidae fam. nov. with any specific lineage of Aculeata.

The same can be said of the wing venation. The fusion of veins C and Sc+R on the forewing is unusual among aculeate wasps. †*Mirabythus* has a relatively well-developed forewing venation, with marginal cell closed, as well as submarginal, medial and second cubital cells enclosed by tubular or nebulous veins. †*Trifionyxius* gen. nov. has a similar condition, except for the marginal cell, which is open distally, and the apparent presence of the 2rs-m enclosing the submarginal cell distally instead of the 2Rs. †*Prionaspidion* gen. nov. exhibits the most reduced forewing venation of the family, without closed cells and a vestigial pterostigma. Simplification of wing venation is a trend within Hymenoptera (Sharkey and Roy 2002; Klopstein et al. 2015), and occurred repeatedly within basal lineages of Aculeata (Melo and Lucena 2020). Assuming monophyly of †Trifionychidae fam. nov., the presence of species with different levels of complexity on forewing venation indicates that the family represents another event of reduction within Aculeata. As far as we could observe, all members of the family lack closed cells in the hind wing, a condition shared with most chrysidoid wasps.

The morphology of the sting apparatus in †Trifionychidae fam. nov. resembles that of Chrysidoidea rather than other aculeate groups. Nevertheless, a furcula is present, differentiating the new family from the clade formed by Dryinidae, Embolemidae and Sclerogibbidae, which completely lacks this structure (Carpenter 1986; Barbosa et al. 2021). This ‘chrysidoid-like’ appearance of their sting is likely due to a plesiomorphic condition, with no obvious similarity with the sting of other aculeate families. Two additional interesting characters possessed by the new family, an undivided and permanently exposed third valvula, are features common with non-aculeate wasps (Smith 1972; Rasnitsyn 1980; Kumpanenko et al. 2019). In aculeate wasps the third valvulae are represented by a pair of sheaths that form a tube allocating the terebra (shaft of the sting), used in assisting its movements, and are kept hidden within the metasoma together with the remainder of the sting apparatus. Although the division of the third valvula in proximal and distal regions is considered as one of the synapomorphies of Aculeata (Rasnitsyn 1980; Ronquist et al. 1999), Barbosa et al. (2021) have shown that in all Chrysidoidea this structure is undivided. Therefore, a divided third valvula should be considered a synapomorphy for Aculeata *s. str.* only (see Kumpanenko et al. 2019 for reversal cases within this group).

The presence of undivided and exposed third valvulae is a characteristic also found in the Mesozoic wasp family †Bethylonymidae, considered as precursors of stinging wasps and frequently recovered as sister group of Aculeata (Rasnitsyn 1975, 1980, 1988; Ronquist et al. 1999; Grimaldi and Engel 2005). Although Rasnitsyn (1975) discarded the presence of sting in †Bethylonymidae and used the exposure of the ovipositor as a character differentiating the family from Aculeata, the structure and conformation of the third valvulae are very similar to what is observed in females of †Trifionychidae fam. nov., especially †*Mirabythus*. In common with †Trifionychidae fam. nov., bethylonymids also exhibit reductions in the number of antennomeres, with a minimum of six flagellomeres in †*Bethylonymellus* (Rasnitsyn 1975). Another character shared at least with some bethylonymids is the fusion of the vein C with Sc+R in the forewing, that can be inferred based on photographs of †*Bethylonymus magnus* Rasnitsyn, 1975 and

†*Bethylonymellus bethyloides* Rasnitsyn, 1975. Unfortunately, this character is difficult to verify in fossils, especially in those from rock impressions, since the anterior margin of the wing may bend or fragment during the process of fossilization.

An important characteristic found in stinging wasps is the third valvula overlapping the terebra distally, with the apical portion of the terebra concealed within the third valvula. This anatomical conformation would facilitate quick and accurate movements of the interlocked first and second valvulae, that compose the terebra (Kumpanenko and Gladun 2017). The ovipositor described and illustrated by Rasnitsyn (1975) for †*Bethylonymidae* apparently exhibit the same conformation, and thus presence of a sting in these wasps cannot be discarded, since the terebra could be hidden between the large third valvulae or be absent due to preservation processes. Presence of sting would indicate that †*Bethylonymidae* are, in fact, the oldest aculeate lineage known from the fossil record. This, in accordance with the plesiomorphic characters of the new family and morphological similarity between †*Trifionychidae* fam. nov. and †*Bethylonymidae*, may indicate that both families are closely related. Alternatively, these families may compose a grade leading to Aculeata, with bethylonymids as sister group to the remaining stinging wasps. Nevertheless, we tentatively maintain †*Trifionychidae* fam. nov. within the superfamily †*Bethylonymoidea*. We consider that reevaluation of the type specimens of †*Bethylonymoidea*, as well as inclusion of species of †*Trifionychidae* fam. nov. in future cladistic analyses will be essential to elucidate the phylogenetic relationships among basal lineages of aculeate Hymenoptera.

Regarding the biological traits of the new family, species of †*Mirabythus* and *Scolebythidae* could have exhibited similar foraging habits, judging by the overall similarity between the body shape of both families. *Scolebythidae* are ectoparasitoids of beetle larvae living concealed within wood (Brothers 1981; Melo 2000), having an elongated and dorso-ventrally flattened body, as well as short and strong appendages. On the other hand, †*Trifionychidae* fam. nov. have been most commonly found in clear amber pieces, without massive amounts of debris. Inclusions in Burmese amber belonging to *Scolebythidae* and †*Holopsenellidae*, among other wasp lineages that presumably attacked wood-boring larvae, are frequently observed in pieces with considerable larger amounts of plant debris and beetle frass (Lepeco and Melo 2022; *personal observation*). Use of beetle larvae living in concealed conditions would be expected for basal clades of Aculeata, since this is considered the groundplan habit for the group (Melo et al. 2011).

Conclusions

We reaffirm the importance of describing the Burmese amber fauna. With the continued study of the ever-increasing amount of material from amber deposits in Myanmar, new insect inclusions have been described, enhancing our knowledge about mid-Cretaceous entomofauna. Observation and description of the new taxa has clarified the identity of †*Mirabythus*, an enigmatic wasp genus originally attributed to the

chrysidoid family Scolebythidae. Perhaps, without the newly described material, we would not be able to infer the non-scolebythid identity of †*Mirabythus*. Nevertheless, the peculiar mosaic of derived and plesiomorphic characters of the new family suggests that the Cretaceous diversity of aculeates may have been composed of many other elements that did not survive to the present day. These lineages are prone to be discovered through deeper investigation of the massive undescribed diversity trapped in Burmese amber. Given the apparent basal position of the new family, untangling its probable behavior will be of great importance to understand the behavioral evolution at early steps of the diversification of aculeate wasps.

Acknowledgements

We sincerely thank Dr. Chung Kun Shih, Dr. Taiping Gao and Ms. Yaping Cai, who kindly provided photographs of the type material of †*Mirabythus* and allowed us to use the photographs in the present publication. We also thank the reviewers Alexandr Rasnitsyn, André Martins and Volker Lohrmann for their careful reading of the manuscript and suggestions to improve it. Financial support has been provided by CNPq.

References

- Aguiar AP, Deans AR, Engel MS, Forshage M, Huber JT, Jennings JT, Johnson NF, Lelej AS, Longino JT, Lohrmann V, Mikó I, Ohl M, Rasmussen C, Taeger A, Yu DSK (2013) Order Hymenoptera. Zootaxa 3701: 51–62. <http://doi.org/10.11646/zootaxa.3703.1.12>
- Azevedo CO, Alencar IDCC, Ramos MS, Barbosa DN, Colombo WD, Vargas JMR, Lim J (2018) Global guide of the flat wasps (Hymenoptera, Bethyridae). Zootaxa 4489: 1–294. <https://doi.org/10.11646/zootaxa.4489.1.1>
- Barbosa DN, Vilhelmsen L, Azevedo CO (2021) Morphology of sting apparatus of Chrysidoidea (Hymenoptera, Aculeata). Arthropod Structure & Development 60: 100999. <https://doi.org/10.1016/j.asd.2020.100999>
- Branstetter MG, Danforth BN, Pitts JP, Faircloth BC, Ward PS, Buffington ML, Gates MW, Kula RR, Brady SG (2017) Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. Current Biology 27: 1019–1025. <https://doi.org/10.1016/j.cub.2017.03.027>
- Brothers DJ (1975) Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. University of Kansas Science Bulletin 50(11): 483–648.
- Brothers DJ (1981) Note on the biology of *Ycaploca evansi* (Hymenoptera: Scolebythidae). Journal of the Entomological Society of Southern Africa 44 (1): 107–108.
- Brothers DJ (1999) Phylogeny and evolution of wasps, ants and bees (Hymenoptera, Chrysidoidea, Vespoidea and Apoidea). Zoologica Scripta 28 (1–2): 233–250. <https://doi.org/10.1046/j.1463-6409.1999.00003.x>

- Brothers DJ (2011) A new Late Cretaceous family of Hymenoptera, and phylogeny of the Plumariidae and Chrysidoidea (Aculeata). *ZooKeys* 130: 515–542. <https://doi.org/10.3897/zookeys.130.1591>
- Brothers DJ, Carpenter JM (1993) Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). *Journal of Hymenoptera Research* 2: 227–304.
- Brothers DJ, Melo GAR (2021) Re-evaluation of the Cretaceous family Plumalexiidae and its relationships (Hymenoptera: Chrysidoidea). *Palaeoentomology* 4(6): 584–591. <https://doi.org/10.11646/palaeoentomology.4.6.7>
- Cai YP, Zhao YY, Shih CK, Ren D (2012) A new genus of Scolebythidae (Hymenoptera: Chrysidoidea) from the Early Cretaceous of China. *Zootaxa* 3504(56): e66. <https://doi.org/10.11646/zootaxa.3504.1.2>.
- Carpenter JM (1986) Cladistics of the Chrysidoidea (Hymenoptera). *Journal of the New York Entomological Society* 94: 303–330.
- Engel MS, Grimaldi DA (2007) Cretaceous Scolebythidae and phylogeny of the family (Hymenoptera: Chrysidoidea). *American Museum Novitates* 3568(2007): 1–16. [https://doi.org/10.1206/0003-0082\(2007\)475\[1:CSAPOT\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2007)475[1:CSAPOT]2.0.CO;2)
- Finnamore AT, Brothers DJ (1993) Superfamily Chrysidoidea. In: Goulet H, Huber JT (Eds) *Hymenoptera of the world: an identification guide to families*. Agriculture Canada Publications (Ottawa): 130–160.
- Grimaldi D, Engel MS (2005) *Evolution of the Insects*. Cambridge University Press, Cambridge.
- Heraty J, Ronquist F, Carpenter JM, Hawks D, Schulmeister S, Dowling AP, Murray D, Munro J, Wheeler WC, Schiff N, Sharkey M (2011) Evolution of the hymenopteran mega-radiation. *Molecular Phylogenetics and Evolution* 60: 73–88. <https://doi.org/10.1016/j.ympev.2011.04.003>
- Huber JT, Sharkey MJ (1993) Chapter 3. Structure. In: Goulet H, Huber JT (Eds) *Hymenoptera of the World: an Identification Guide to Families*. Agriculture Canada Publication, Ottawa, 13–59.
- Johnson BR, Borowiec ML, Chiu JC, Lee EK, Atallah J, Ward PS (2013) Phylogenomics resolves evolutionary relationships among ants, bees, and wasps. *Current Biology* 23(20): 2058–2062. <https://doi.org/10.1016/j.cub.2013.08.050>
- Kawada R, Buffington ML (2016) A scalable and modular dome illumination system for scientific microphotography on a budget. *PLoS ONE* 11(5): e0153426. <https://doi.org/10.1371/journal.pone.0153426>
- Klopfstein S, Vilhelmsen L, Ronquist F (2015) A nonstationary Markov model detects directional evolution in hymenopteran morphology. *Systematic biology* 64(6): 1089–1103. <https://doi.org/10.1093/sysbio/syv052>
- Kumpanenko AS, Gladun DV (2018) Functional morphology of the sting apparatus of the spider wasp *Cryptocheilus versicolor* (Scopoli, 1763) (Hymenoptera: Pompilidae). *Entomological Science* 21(1): 124–132. <https://doi.org/10.1111/ens.12288>.
- Kumpanenko A, Gladun D, Vilhelmsen L (2019) Functional morphology and evolution of the sting sheaths in Aculeata (Hymenoptera). *Arthropod Systematics & Phylogeny* 77(2): 325–338.

- Lepeco A, Melo GAR (2022) The wasp genus †*Holopsenella* in mid-Cretaceous Burmese amber (Hymenoptera: †Holopsenellidae stat. nov.). *Cretaceous Research* 131: 105089. <https://doi.org/10.1016/j.cretres.2021.105089>
- Li L, Rasnitsyn AP, Shih C, Li D, Ren D (2020) Two new rare wasps (Hymenoptera: Apocrita: Panguidae and Burmusculidae) from mid-Cretaceous amber of Northern Myanmar. *Cretaceous Research* 109: 104220. <https://doi.org/10.1016/j.cretres.2019.104220>
- Liu SI (2018) Burmese Amber from Khamti, Sagaing Region. *The Journal of Gemmology* 36(2): 107–111.
- Lucena DA, Almeida EAB (2022) Morphology and Bayesian tip-dating recover deep Cretaceous-age divergences among major chrysidid lineages (Hymenoptera: Chrysididae). *Zoological Journal of the Linnean Society* 194(1): 36–79. <https://doi.org/10.1093/zoolinnean/zlab010>
- Melo GAR (2000) Biology of an extant species of the scolebythid genus *Dominibythus* (Hymenoptera: Chrysidoidea: Scolebythidae), with description of its mature larva. In: Austin AD, Dowton M (Eds) *Hymenoptera: evolution, biodiversity and biological control*, CSIRO Collingwood, 281–284.
- Melo GAR, Lucena DAA (2020) †Chrysobythidae, a new family of chrysidoid wasps from Cretaceous Burmese amber (Hymenoptera, Aculeata). *Historical Biology* 32(8): 1143–1155. <https://doi.org/10.1080/08912963.2019.1570184>
- Melo GAR, Hermes MG, Garcete-Barrett BR (2011) Origin and occurrence of predation among Hymenoptera: a phylogenetic perspective. In: Polidori C (Ed.) *Predation in the Hymenoptera: an evolutionary perspective*. Trivandrum: Transworld Research Network, 1–22.
- Oeser R (1961) Vergleichend-morphologische Untersuchungen über den Ovipositor der Hymenopteren. *Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologisches Museum und Institut für Spezielle Zoologie (Berlin)* 37(1): 3–119. <https://doi.org/10.1002/mmzn.19610370102>
- Pauli T, Meusemann K, Kukowka S, Sann M, Donath A, Mayer C, Oeyen JP, Ballesteros Y, Berg A, Van den Berghe E, Escalona HE, Guglielmino A, Niehuis M, Olmi M, Podsiadlowski L, Polidori C, De Rond J, Rosa P, Schmitt T, Strumia F, Wurdack M, Liu S, Zhou X, Misof B, Peters RS, Niehuis O (2021) Analysis of RNA-Seq, DNA target enrichment, and Sanger nucleotide sequence data resolves deep splits in the phylogeny of cuckoo wasps (Hymenoptera: Chrysididae). *Insect Systematics and Diversity* 5: 1–14. <https://doi.org/10.1093/isd/ixaa018>
- Perkovsky EE, Martynova KV, Mita T, Olmi M, Zheng Y, Müller P, Zhang Q, Gantier F, Perichot V (2020) A golden age for ectoparasitoids of Embiodea: Cretaceous Sclerogibbidae (Hymenoptera, Chrysidoidea) from *Kachin* (Myanmar), *Charentes* (France) and *Choshi* (Japan) ambers. *Gondwana Research* 87: 1–22. <https://doi.org/10.1016/j.gr.2020.06.004>
- Peters RS, Krogmann L, Mayer C, Donath A, Gunkel S, Meusemann K, Kozlov A, Podsiadlowski L, Petersen M, Lanfear R, Diez PA, Heraty J, Kjer KM, Klopstein S, Meier R, Polidori C, Schmitt T, Liu S, Zhou X, Wappler T, Rust J, Misof B, Niehuis O (2017) Evolutionary history of the Hymenoptera. *Current Biology* 27: 1013–1018. <https://doi.org/10.1016/j.cub.2017.01.027>
- Pilgrim EM, Von Dohlen CD, Pitts JP (2008) Molecular phylogenetics of Vespoidea indicate paraphyly of the superfamily and novel relationships of its component families

- and subfamilies. *Zoologica Scripta* 37(5): 539–560. <https://doi.org/10.1111/j.1463-6409.2008.00340.x>
- Prentice MA, Poinar Jr GO, Milki R (1996) Fossil scolybythids (Hymenoptera: Scolybythidae) from Lebanese and Dominican amber. *Proceedings of the Entomological Society of Washington* 98(4): 802–811.
- Rasnitsyn AP (1975) Vysshie pereponchatokrylyie mezozoya [Hymenoptera Apocrita of Mesozoic]. *Transactions of the Palaeontological Institute* 147: 1–133.
- Rasnitsyn AP (1980) Origin and evolution of Hymenoptera. *Transactions of the Paleontological Institute of the Academy of Sciences of the USSR* 174: 1–192.
- Rasnitsyn AP (1988) An outline of evolution of the hymenopterous insects (order Vespida). *Oriental Insects* 22(1): 115–145. <https://doi.org/10.1080/00305316.1988.11835485>
- Rasnitsyn AP, Bashkuev AS, Kopylov DS, Lukashevich ED, Ponomarenko AG, Popov YA, Rasnitsyn DA, Ryzhkova OV, Sidorchuk EA, Sukatsheva ID, Vorontsov DD (2016) Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). *Cretaceous Research* 61: 234–255. <https://doi.org/10.1016/j.cretres.2015.12.025>
- Rasnitsyn AP, Zhang Q, Müller P, Zhang HC (2020) On the identity and limits of Falsiformicidae (Insecta: Hymenoptera, Vespoidea sl). *Palaeoentomology* 3(6): 582–596. <https://doi.org/10.11646/PALAEOENTOMOLOGY.3.6.10>
- Rodriguez J, Waichert C, Von Dohlen CD, Poinar GO, Pitts JP (2015) Eocene and not Cretaceous origin of spider wasps: Fossil evidence from amber. *Acta Palaeontologica Polonica* 61(1): 89–96. <https://doi.org/10.4202/app.00073.2014>
- Ronquist F, Rasnitsyn AP, Roy A, Eriksson K, Lindgren M (1999) Phylogeny of the Hymenoptera: a cladistic reanalysis of Rasnitsyn's (1988) data. *Zoologica Scripta* 28(1–2): 13–50. <https://doi.org/10.1046/j.1463-6409.1999.00023.x>
- Rosa BB, Melo GAR (2021) Apoid wasps (Hymenoptera: Apoidea) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research* 122: 104770. <https://doi.org/10.1016/j.cretres.2021.104770>
- Sharkey MJ, Roy A (2002) Phylogeny of the Hymenoptera: a reanalysis of the Ronquist et al. (1999) reanalysis, emphasizing wing venation and apocritan relationships. *Zoologica Scripta* 31(1): 57–66. <https://doi.org/10.1046/j.0300-3256.2001.00081.x>
- Shi GH, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang MC, Lei WY, Li QL, Li XH (2012) Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37: 155–163. <https://doi.org/10.1016/j.cretres.2012.03.014>.
- Smith EL (1972) Biosystematics and morphology of Symphyta – III. External genitalia of *Euura* (Hymenoptera: Tenthredinidae): sclerites, sensilla, musculature, development and oviposition behavior. *International Journal of Insect Morphology and Embryology* 1(4): 321–365. [https://doi.org/10.1016/0020-7322\(72\)90016-5](https://doi.org/10.1016/0020-7322(72)90016-5)
- Snodgrass RE (1935) *Principles of Insect Morphology*. McGraw-Hill publications in the zoological sciences, New York/London.
- Vilhelmsen L, Miko I, Krogmann L (2010) Beyond the wasp-waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). *Zoological Journal of the Linnean Society* 159(1): 22–194. <https://doi.org/10.1111/j.1096-3642.2009.00576.x>

- Xing L, Qiu L (2020) Zircon U-Pb age constraints on the mid-Cretaceous Hkamti amber biota in northern Myanmar. *Palaeogeography, Palaeoclimatology, Palaeoecology* 558: 109960. <https://doi.org/10.1016/j.palaeo.2020.109960>.
- Zhang Q, Rasnitsyn AP, Zhang H (2018a) *Burmusculidae*, a new and basal family of pompiloid wasps from the Cretaceous of Eurasia (Hymenoptera: Pompiloidea). *Cretaceous Research* 91: 341–349. <https://doi.org/10.1016/j.cretres.2018.07.004>
- Zhang Q, Rasnitsyn AP, Wang B, Zhang H (2018b) Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: a review of the fauna. *Proceedings of the Geologists' Association* 129(6): 736–747. <https://doi.org/10.1016/j.pgeola.2018.06.004>

Supplementary material I

Additional figures of †*Mirabythus lechrius* Cai et al., 2012 and †*Mirabythus liae* Cai et al., 2012.

Authors: Anderson Lepeco, Diego N. Barbosa, Gabriel A. R. Melo

Data type: images (zip file)

Explanation note: †*Mirabythus lechrius* Cai et al., 2012, dorsal view of head and mesosoma, †*Mirabythus lechrius* Cai et al., 2012, dorsal view of head, †*Mirabythus lechrius* Cai et al., 2012, detail of clypeus. †*Mirabythus liae* Cai et al., 2012, habitus, dorsal view, †*Mirabythus liae* Cai et al., 2012, dorsal view of head.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.94.85613.suppl1>